SPATIAL VARIATION IN BLUEBERRY (*VACCINIUM ULIGINOSUM*) AND LINGONBERRY (*VACCINIUM VITIS-IDAEA*) FRUIT PRODUCTION IN INTERIOR ALASKA

By

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Abstract

There are over 50 species of plants in Alaska that produce fleshy fruits (hereafter: "berries"), of which people consume 25. Berries are a key cultural and nutritional resource in rural Alaska and an important source of calories for a range of animals including bears (*Ursus spp.*), foxes (*Vulpes vulpes),* geese (e.g., *Branta hutchinsii*), and voles (e.g., *Myodes rutilus*). Berry production, from bud development to ripe fruit, takes at least 15 months and may be affected by factors even a year or two before that. Many studies in the circumpolar North focus on these interannual effects on fruit production but few assess how local variation within a forested region may affect berry numbers. Changes in the frequency and severity of wildfires in the boreal forest has affected soil conditions and plant community structure, which may alter the range of circumstances a species must respond to, influencing overall fruit production at a site. I studied how fruit production in *Vaccinium uliginosum* (blueberry) and *V. vitis-idaea* (lingonberry), responded to factors such as pollen load, floral resources, canopy cover, and soil conditions within forest sites of Interior Alaska. I found two distinct habitat types in the Interior Alaskan forest, upland and lowland, which differed by elevation, soil moisture (lower in upland sites), and active layer (deeper in upland sites). We found lingonberry was more pollen limited than blueberry, and plants in lowland sites were more pollen limited while plants in upland sites were more resource limited. Additionally, canopy cover had a significant negative effect on a ramet's investment in flowers, berries, and leaves, versus structural growth, in upland sites but little effect in lowland sites. I was able to explain more of the variation in berry production and resource allocation in upland sites than lowland sites. Pollen and resource limitation differed between the two species and between uplands and lowlands suggesting *Vaccinium* berry production and resource allocation is partially defined by spatial variability of the landscape.

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Chapter 1 General introduction

1.1 Interior Alaska

In Interior Alaska, the central region of the state bordered by the Alaska Range to the south and the Brooks Range to the north, wild fruits are crucial to animals and people. Each year in Alaska over 50 species of plants produce fleshy fruits (hereafter: "berries"; Hultén 1968). Berries are a vital source of plant-based nutrients in rural Alaska (Johnson et al. 2009). As one of the few sources of concentrated sugars in the sub-Arctic and Arctic, berries are an important source of calories for a range of animals including bears (*Ursus spp.*), foxes (*Vulpes vulpes),* geese (e.g., *Branta hutchinsii*), and voles (e.g., *Myodes rutilus*) (e.g., Weeden 1969; Hatler 1972; West 1982; Hupp et al. 2013; Stenset et al. 2016). In aggregate, people throughout Alaska use around half of the 50 berry species in the state for food or medicine (Hupp et al. 2015). In 2015, rural communities in Interior Alaska collected a mean of 3.4 kg of berries per person (individual communities ranged from 0.85 to 9.3 kg/person) (ADFG 2015). Subsistence harvesters have expressed the need to understand how climate change may influence the availability of species traditionally hunted, fished, and gathered, including berries (Loring and Gerlach 2009; Knapp and Trainor 2015; Hupp et al. 2015).

The berry species of Interior Alaska are a small component of the boreal ecoregion that covers ⅓ of the state of Alaska (Nowacki et al. 2001). One third of the boreal ecoregion is forested (42.8 million hectares), of which 70% is dominated by black spruce (*Picea mariana* Mill.) (Viereck and Little 1975; Nowacki et al. 2001). Black spruce forests vary in geography, fire history, and plant community. Each of these components may affect berry growth but many studies assessing boreal berry productivity focus on the influences and predictors of interannual

variability across a forested region as opposed to the factors affecting spatial variability in fruit production within the region (e.g., Krebs et al. 2009; Ihalainen et al. 2003).

This thesis focuses on two fruit-producing species that are particularly important in Interior Alaska: *Vaccinium uliginosum* L. (lowbush blueberry, bog blueberry, bog bilberry, hereafter: blueberry) and *V. vitis-idaea* L. (lowbush cranberry, cowberry, partridgeberry, lingonberry, hereafter: lingonberry). The fruits, and the plants, make up the base of many food chains. For example, around 10% of Interior Alaskan snowshoe hare (*Lepus americanus*) diet in spring and fall is *Vaccinium* leaves (Wolff 1978). Red-backed voles (*Myodes rutilus*) rely heavily on berries all year (West 1982). In the Yukon Territory of Canada, 95% of bear scat volume was berries and other plant material in spring and summer (MacHutchon 1989). In turn, animals such as voles and hares make up the diet of a number of predators (e.g., Nelson et al. 2008). Blueberry and lingonberry are the two species most commonly picked by people in Interior Alaska (Hupp et al. 2015). Nearly three quarters of all berries collected in rural communities in the Interior are from these two species (e.g., in 2015, mean harvest was 1.5 kg/person of blueberries and 0.99 kg/person of lingonberries; ADFG 2015).

Due to anthropogenically-driven climate change, the boreal forest environment is experiencing novel situations: surface moisture has declined throughout the circumpolar north, particularly in Alaska and western Canada (Serreze et al. 2000), while fire activity has increased (resulting in a greater area burned, lengthened fire season and increased fire severity) (Turetsky et al. 2011). The increase in burned soil organic layer is linked to a greater likelihood of deciduous as opposed to spruce regeneration on the landscape (Johnstone and Kasischke 2005, Johnstone et al. 2010, Beck et al. 2011). This could lead to a prolonged shift in vegetation patterns in parts of the boreal forest. By studying how *V. uliginosum* and *V. vitis-idaea*

reproduction and resource allocation vary across the black spruce forest of Interior Alaska, I hope to assist in efforts to predict how this subsistence resource may respond to future changes.

1.2 *Vaccinium* species in black spruce forest

The boreal forest forms a ring through the midst of the circumpolar north, spanning Alaska, Canada, Scandinavia, and Russia, encompassing one third of the world's forested land (Shugart et al. 1992), and covering the second largest area of any terrestrial biome (Pielou 1988). Discontinuous permafrost underlies much of the forest and plays a large role in determining species composition, and nutrient and hydrological cycles (e.g., Péwé 1975; Brown et al. 1997; Osterkamp et al. 2000). Cold air and soil temperatures also influence species' range limits (e.g.,Van Cleve et al. 1991). Seventy percent of Interior Alaska forest cover is dominated by black spruce, the rest is primarily white spruce (*Picea glauca* (Moench) Voss), and deciduous trees such as Alaskan birch (*Betula neoalaskana* Sarg.), quaking aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.) (Viereck et al. 1986; Chapin et al. 2006). Ericaceous shrubs *Rhododendron groenlandicum* L., *Vaccinium vitis-idaea* and *V. uliginosum* are dominant species in the understory (Hultén 1968) along with feather mosses and lichens (Oechel and Van Cleve 1986).

Landscape level influences on plant community structure in boreal black spruce forest include slope, aspect, elevation, and fire frequency. North-facing slopes have cold, poorly drained soils underlain with permafrost, and are primarily composed of black spruce stands with a moss understory (Viereck et al. 1983, Van Cleve et al. 1991). South facing aspects tend to have warmer, well drained soils occupied by deciduous trees and white spruce (Viereck et al. 1983). Slope, aspect, and elevation are stable influences on plant communities but wildfires are getting larger and return more quickly, across not only Alaska but much of North America's boreal

forest regions (Weber and Flannigan 1997; Kasischke and Turetsky 2006; Kasischke et al. 2010). As the primary driver of landscape heterogeneity, fire shapes ecosystem dynamics, plant communities, and populations.

Blueberry and lingonberry are two berry-producing shrubs with a broad distribution across the Alaskan boreal forest (Hultén 1968). Both are long-lived, rhizomatous clonal shrubs that tend to grow in patches (Hultén 1968) but they use different life history strategies. Blueberry are deciduous and grow 10–75 cm tall. Lingonberry plants are evergreen, their leaves have a waxy coating and last up to three years (CPH Mulder, unpublished data), and ramets grow 10 to 40 cm in height/length (Douglas et al. 2000). *V. uliginosum* grows in the western and northern continental United States, Alaska, Canada, Greenland, and parts of Europe and Asia, while *V. vitis-idaea* has a still wider range across the circumpolar North in a variety of environments within the boreal forest and tussock tundra (Hultén 1968; Viereck and Little 1975, Tirmenstein 1991). If there are long stretches without a forest fire blueberry and lingonberry are encroached upon by other understory plants including black crowberry (*Empetrum nigrum*) and feather mosses (*Pleurozium* and *Hylecomium spp.)* (Oechel and Van Cleve 1986; Turetsky et al. 2010).

1.2.1 Factors affecting Vaccinium *reproduction*

Fruit production in all plants is limited by four broad factors: 1) external pulses such as predation, disease, or harsh weather; 2) genetics; 3) pollination; and 4) resources such as soil nutrients and light (Stephensen 1981; Charlesworth 1989; Ehrlen 1992). *Vaccinium* flower buds that open in a given growing season were initially created by the plant at least one year before and their abundance could be influenced by a good growing season even a year before that (1-2 years ahead of when they actually flower) (Krebs et al. 2009; Mulder et al. 2017). Thus, berry production in a particular year may be influenced by weather, pathogens, or herbivores

negatively affecting plant growth and bud development at any point in the years preceding flowering. Roy and Mulder (2014) found that lingonberry populations around Interior Alaska, while not continuous, show little sign of genetic differentiation so major genetic differences are likely not the cause of changes in berry production. In this thesis I focus on factors directly involved during the growing season in which the *Vaccinium* flowered: pollination and resource availability.

There tend to be fewer pollinators and flowering species, as well as a shorter flowering period, in boreal forest ecosystems than in other forest types (Kevan et al. 1993). Pollinator activity is influenced by flower abundance, temperature, or availability of pollinator nesting sites (Westrich 1996; Gathmann and Tscharntke 2002; Westphal et al. 2003; Bartomeus et al. 2010). Both *V. uliginosum* and *V. vitis-idaea* are self-compatible but the structure of the flowers limits selfing (Reader 1977) and even when self-pollination occurs there is a significant reduction in fruit set (the ratio of fruits to flowers) (Nuortlina et al. 2002). When pollinators were denied access to flowers, there was a 76% reduction in blueberry fruit set and 94% reduction in lingonberry fruit set compared to flowers with pollinator access (Spellman et al. 2015; CPH Mulder unpublished data). In Interior Alaska, species capable of buzz pollination such as bumblebees (*Bombus spp.*), syrphid flies (*Syrphidae)*, and solitary bees (*Andrena spp.*) carry the most *Vaccinium* pollen (Davis et al. 2003), although pollinators such as butterflies (*Lepidoptera*) and beetles may transfer pollen as well (Davis et al. 2002).

As with other Northern dwarf shrubs, *V. uliginosum* and *V. vitis-idaea* are adapted to low nutrient levels with little capacity to use any added nutrients (Chapin et al. 1986). In Finland both the European bilberry (*V. myrtillus*) and the lingonberry produced more flower buds in open habitats where light was abundant (Tolvanen 1995). Additionally, *Vaccinium* ramets in more

open habitats may be better able to compensate after herbivory due to higher photosynthetic rates (Dudt and Shure 1994). In a Russian wildfire chronosequence, blueberry and *V. oxycoccus* (bog cranberry) began fruiting 3 years after the fire. Blueberry yield was more than 2 times as high in the burned region as compared to the unburned control a year after fruiting began (Mironov 1984, in Nelson et al. 2008). The authors attributed the increased growth to increased light availability (Mironov 1984, in Nelson et al. 2008).

Definitively identifying pollen and resource limitation is difficult under natural conditions (Griffin and Barrett 2002; Huang and Guo 2002) but researchers across the circumpolar North have investigated components of *Vaccinium* berry production in an attempt to tease apart relative influences. Fruit abundance is strongly correlated with pollinator activity but location of the berry plant within the landscape is also important as location affects a ramet's sensitivity to weather fluctuations (Boulanger-LaPointe et al. 2017; Barber et al. 2016). One study found plants in open environments are more susceptible to changes in air temperature, with low elevation *Vaccinium* producing fewer berries in cool summers, while another found it is the intensity of solar radiation within landscape types that affects berry production (Boulanger-LaPointe et al. 2017; Barber et al. 2016). Huckleberries (*V. membranaceum)* in Alberta, Canada are limited by terrain and moisture availability while pollen availability was the strongest determinant of boreal berry production according to models of Finnish bilberry (*V. myrtillus)* (Barber et al. 2016; Boulanger-LaPointe et al. 2017). While we can draw many parallels between European and Alaskan boreal forests, the pine-dominated forests of Europe where much of the berry research has taken place have been managed for timber as well as non-timber forest products for hundreds of years (Östlund et al. 1997). The spatial structure of many Scandinavian forests is dictated by human economic needs rather than natural succession (Östlund et al. 1997).

Berries in the spruce-dominant, relatively unmanaged forests of Alaska may be responding to different pollinator or environmental conditions.

1.2.2 The role of resource allocation

Vaccinium ramets have a highly plastic morphology that may help the plants respond to changes in their environments and persist at the sites they have already occupied as the forest grows up around them (Tolvanen 1995). The leaf economic spectrum states that with limited resources available there are only a few investment strategies that will lead to a positive fitness outcome. The spectrum ranges from low investment with quick return by creating leaves with a high specific leaf area and low life spans (e.g., broadleaved deciduous trees) to leaves with low specific leaf area but much longer life spans (e.g., evergreen trees with needle-shaped leaves) (Reich et al. 2003; Wright et al. 2005; Shipley et al. 2006). Plant species with a high specific leaf area also tend to have lower stem density (Méndez-Alonzo et al. 2012), less allocation to roots, higher root N concentrations, and a higher rate of nutrient uptake given root mass compared to those species with a low specific leaf area (Lambers and Poorter, 1992). Berry plants may not differ solely in fruit production due to environmental conditions but also in resource allocation between flower and leaf growth. Reproduction is a costly function for plants so relative allocation towards reproduction may increase or decrease as external conditions change. Additionally, which environmental components limit or determine allocation may differ by species or spatially across the boreal forest.

Tolvanen (1995) investigated growth habits (branching architecture, bud formation, and flowering frequency) of *V. myrtillus* (a close relative of *V. uliginosum)* and *V. vitis-idaea* with respect to age and habitat type in an open spruce forest and a clearcut in northern Finland. While Tolvanen did establish that there were morphological differences between forested and open sites

and that ramets alternated between reproductive and vegetative growth, she did not measure the extent of those investment tradeoffs between leaf and berry development or the environmental components of variation.

1.3 Moving ahead

This thesis aims to explore how fruit production and resource allocation in *Vaccinium vitis-idaea* and *Vaccinium uliginosum* respond to spatial variability in environmental factors such as pollen and resource availability within the Alaskan boreal forest. My research on spatial variation complements existing research on temporal variation in *Vaccinium* reproduction to provide a foundation for others to model berry crops for humans and animals in the future.

Chapter Two investigates the relationship between a range of landscape characteristics representative of a variety of black spruce successional stages and *Vaccinium* fruit set. Specifically, I use structural equation modeling to look at the effects of site geography and fire history on flower and fruit production within a single summer. I then build on the findings of spatial differentiation in reproduction to compare blueberry and lingonberry investment in reproduction versus growth by comparing biomass ratios of blueberry and lingonberry ramets to investigate the conditions that drive allocation.

In the conclusion chapter, I expand upon the variation I found in berry production and resource allocation between species and habitat types in the context of interannual research and local observations of berry production. I speculate briefly on possible future research directions and effects on berry availability for humans and animals in Interior Alaska given what we know of changes in vegetation and fire history.

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Chapter 2 Spatial variability in pollen and resource limitation in two boreal fruit producing species: *Vaccinium uliginosum* and *V. vitis-idaea*[1]

2.1 Abstract

Many recent studies assessing fruit productivity of plants in the boreal forest focus on interannual variability across a forested region, rather than environmental variability within the forest. Changes in the frequency and severity of wildfires in the boreal forest has affected soil moisture, canopy, and community structure, all of which may alter the range of conditions a species must respond to and influence overall fruit production at a site. We evaluated how fruit production in two boreal shrubs, *Vaccinium uliginosum* (blueberry) and *V. vitis-idaea* (lingonberry), responded to factors such as pollen load, floral resources, canopy cover, and soil conditions within boreal forest sites of Interior Alaska. We classified our study sites into upland and lowland, which differed by elevation, soil moisture (lower in upland sites), and active layer (deeper in upland sites). Pollen and resource limitation differed between the two species and between uplands and lowlands. Our results suggest *Vaccinium* berry production is limited through a mix of pollen and resource limitation defined by spatial variability of the landscape. We found lingonberry was more pollen limited than blueberry, and plants in lowland sites were more pollen limited while plants in upland sites were more resource limited. Additionally, canopy cover had a significant negative effect on a ramet's investment in reproductive tissues and leaves, versus structural growth, in upland sites but little effect in lowland sites.

[1] Parkinson, L.V., and Mulder, C.P.H. Spatial variability in pollen and resource limitation in two boreal fruit producing species: *Vaccinium uliginosum* and *V. vitis-idaea.* Prepared for submission to *Botany.*

2.2 Introduction

At least 50 species of plants produce fleshy fruits (hereafter: "berries") in Alaska (Hultén 1965). In Interior Alaska, a region bordered by the Alaska Range to the south and the Brooks Range to the north, *Vaccinium vitis-idaea* L. (lingonberry, cowberry, partridgeberry, lowbush cranberry, hereafter: lingonberry) and *V. uliginosum* L. (lowbush blueberry, bog bilberry, bog blueberry, hereafter: blueberry), are two of the most commonly consumed fruits by both humans and animals (Hupp et al. 2015). Many species including bears (*Ursus spp.*), foxes (*Vulpes vulpes),* geese (e.g., *Branta hutchinsii*), and voles (e.g., *Myodes rutilus*) eat the berries (e.g., Weeden 1969; Hatler 1972; West 1982; Hupp et al. 2013; Stenset et al. 2016). Nearly three quarters of all berries collected in rural communities in Interior Alaska in 2015 were from these two species, with a mean of 1.5 kg/person of blueberries and 0.99 kg/person of lingonberries (ADFG 2015). Berry production is a multi-year process dependent upon weather, pollinator activity, light availability, and soil conditions (Kuchko 1988; Yudina and Maksimova 2005). Recent studies assessing berry production in boreal plants have focused on interannual variability across a region (Krebs et al. 2009; Ihalainen et al. 2003) but berry production varies spatially within the region as well (Tolvanen 1995; Barber et al. 2016). Due to the multi-year development period of *Vaccinium* flowers, interannual models of fruit production account for some of the effects of changing weather and climate; however, abiotic factors that affect spatial variability are often overlooked.

Understanding how *Vaccinium* berry production responds to heterogeneous environmental factors such as variation in resource availability (limiting growth and berry development) and variation in pollinator availability (limiting fertilization) within Alaska's boreal forest can provide a foundation for modelling berry crops for humans and animals (i.e.

where on the landscape we would expect more berry production). Models assessing how changes in wildfire, soil moisture, and permafrost in Interior Alaska may affect plant community structure, including *Vaccinium* growth, already exist (e.g., Yuan et al. 2007; Rupp et al. 2015; Anstedt 2011; SNAP 2018). However, vegetative plant growth and fruit availability are not always correlated (Johnson et al. 1995). Fruit production in all plants is limited by four factors: 1) genetics 2) external pulses such as herbivory, disease, or harsh weather 3) pollination and 4) resources (e.g., light and soil moisture) (Stephenson 1981; Charlesworth 1989; Ehrlen 1992). This paper will focus on resource and pollen limitation.

Slope, aspect, elevation, and fire frequency influence plant community structure in the boreal zone (Viereck et al. 1983; Van Cleve et al. 1991; Hollingsworth et al. 2006). North-facing slopes receive limited sunlight, have cold, poorly drained soils underlain with permafrost, and are primarily composed of *Picea mariana* (black spruce) stands with a moss understory (Viereck et al.1983, Hollingsworth et al. 2006). South facing aspects tend to have warmer, well drained soils occupied by deciduous trees and *P. glauca* (white spruce) (Viereck et al. 1983; Van Cleve et al. 1991). Slope, aspect, and elevation have not changed over the past century but wildfires are getting larger and returning more quickly across North America's boreal forest regions (e.g., Weber and Flannigan 1997; Kasischke and Turetsky 2006; Kasischke et al. 2010). As a driver of vegetative heterogeneity, fire shapes ecosystem dynamics including plant succession and soil condition. In most situations, low shrubs (including many of the berry species of Interior Alaska) are the dominant cover for a decade or two after a fire. Tall shrubs and deciduous trees begin to take over and the canopy closes limiting the light available (Messier et al. 1998). If the seed bank survived the wildfire, deciduous trees generally give way to secondary successional black spruce and the canopy opens again (Viereck et al. 1983; Van Cleve et al. 1991).

The leaf economic spectrum illustrates that with limited resources available there are only a few investment strategies that will lead to a positive fitness outcome. The spectrum ranges from plants that are selected for low investment with quick return by creating leaves with a high specific leaf area (leaf surface area per gram dry leaf tissue) and low life spans (e.g., broadleaved deciduous trees) to leaves with low specific leaf area but much longer life spans (e.g., evergreen trees with needle-shaped leaves) (Reich et al. 2003; Wright et al. 2005; Shipley et al. 2006). Additionally, plants trade-off between immediate survival, via vegetative growth, and long-term gene transfer, via reproductive growth. Species with a low maximum relative growth rate (biomass increase per unit existing biomass per unit time) are generally found in stressful environments, whereas species with higher relative growth rates are generally in more favorable environments (Grime 1977). A species' ability to efficiently respond to changes in canopy conditions vegetatively may give an advantage reproductively. Lingonberries produce thick, evergreen leaves that last about three years (CPH Mulder, unpublished data) and replace 39% of standing biomass each year, while blueberries produce deciduous leaves and have an annual turnover of 62% standing biomass (Wardle and Zackrisson 2005). As such, blueberries fall closer to the resource acquisitive end of the spectrum, potentially able to respond to changes in habitat conditions more quickly than lingonberries on the resource conservative end. Blueberry shrubs may be able to create leaves better suited to each growing season than lingonberry, affecting investment by the two species in growth versus reproduction.

Black spruce forests on north facing and lowland sites are typically underlain by permafrost, which leads to cold, wet soils with relatively low nutrient availability (Hollingsworth et al. 2006). Interior Alaska is underlain with discontinuous permafrost which changes the soil moisture conditions above it by impeding soil drainage in some locations but not others (Viereck

et al. 1983; Chapin et al. 2006). Saturated soils are likely to have a negative effect on nutrient availability due to anoxia reducing microbial activity. The presence of shallow permafrost cools the soil and inhibits drainage so water collects from weather events through the growing season as well as from the thawing ground. Fires can remove much of the moss and soil layer that insulates the permafrost, drastically changing the active layer (the layer that freezes and thaws annually) depth and thus moisture and temperature conditions of the forest stand (Yoshikawa et al. 2002).

Environmental variation may affect berry production directly, through a plant's responses to changes such as those discussed above, or indirectly through effects on pollinators. Pollinator and floral diversity are low in the boreal forest so many flowers receive multiple pollinators and those pollinators visit many flower species (Kevan et al. 1993). In Interior Alaska, bumblebees (*Bombus spp.*), syrphid flies (*Syrphidae*), and solitary bees (*Adrena spp.*) carry the most blueberry and lingonberry pollen (Davis et al. 2003; Holloway 2006). Sites with more flowers in the neighborhood may lure pollinators away from the *Vaccinium* ramets, as suggested by the floral market hypothesis, but could also draw pollinators into the area that otherwise would not have visited (Chittka and Schürkens 2001). Pollen availability explains the most variation in Finnish bilberry (*V. myrtillus*) fruit production models (Boulanger-LaPointe et al. 2017).

We assessed the relative effects of light, nutrient resources, and pollen availability on berry production and resource allocation in the boreal forest around Interior Alaska. We hypothesized that multiple variables would directly affect berry production and also expected interactions among predictors. Specifically:

1. Stand history (time since last fire) was expected to be the primary driver of environmental resource limitation. Fires remove much of the overstory, providing the

understory with access to direct light for 10-20 years before deciduous saplings, and later spruce, begin to limit access to light.

2. Total floral resources (the number of flowers in the vicinity) was expected to have a positive influence on pollen load and thus berry production as a greater number of flowers in the area would attract more pollinators.
3. Berry fruit set (the ratio of fruits to flowers) was expected to be more limited by light availability than pollen availability due to the added direct and indirect effects of canopy cover.
4. Blueberry ramets' relative biomass allocation towards reproduction were expected to be more responsive to changes in canopy cover than lingonberries' due to the differences in the two plants' life history strategies.

2.3 Methods

2.3.1 Study area and site selection

About one third of the Interior Alaska boreal ecoregion is forested, with 70% of forest cover dominated by black spruce *(Picea mariana* Mill.); the rest is primarily white spruce (*P. glauca* (Moench) Voss), and deciduous trees such as Alaskan birch (*Betula neoalaskana* Sarg.), quaking aspen (*Populus tremuloides* Michx.), and balsam poplar (*P. balsamifera* L.) (Viereck and Little 1975; Viereck et al. 1986, Chapin et al. 2006). Ericaceous shrubs such as Labrador tea (*Rhododendron groenlandicum* L.), blueberry, and lingonberry are dominant species in the understory (Hultén 1968). This study focused on black spruce stands that span 13 to 200 years since last fire (stand age) and vary in slope, aspect, and forest structure to encompass a variety of growing conditions for *Vaccinium* (Appendix A). We evaluated berry production at 17 sites within the Bonanza Creek LTER Regional Site Network where previous studies found both

blueberry and lingonberry ramets (Ruess et al. 2015) and which were accessible by foot or all-terrain vehicle during early summer (Figure 2.1). The regional site network encompasses a range of boreal forest types designed to represent the variability in community composition and successional processes around Interior Alaska (Appendix A).

2.3.2 Plant selection

From the center of each site we marked the nearest flowering *Vaccinium* ramet to a set of 12 randomly generated coordinates composed of compass degree (0-359°) and distance (0-20 m), with a search area up to 2 m. If we tagged a ramet too early in the season to distinguish fully between flower and leaf buds, and on the next visit it was clear the ramet was non-reproductive, we moved the tag to the nearest conspecific with distinguishable flower buds. Sites without flowering lingonberry or blueberry within our random points were thoroughly searched and any reproductive blueberry or lingonberry ramets were tagged. We monitored 186 blueberry ramets (mean 10.6 tagged reproductive ramets per site, range: 1-12 tagged ramets across sites) and 194 lingonberry ramets (mean: 11.3 tagged reproductive ramets per site, range: 2-12 ramets across the sites) in total. We counted the number of berries produced when the berries at each site began to ripen. Depending on the site and the species, counts took place from mid-July to early August.

2.3.3 Hypothesized drivers of berry production

We used five variables, measured at the site level, to investigate spatial variability and resource limitation: elevation, active layer depth, time since fire (stand age), soil moisture, and soil temperature. Active layer depth and time since fire are both positively related to soil nutrient availability while soil moisture is negatively related to nutrient availability in Interior Alaska (Allison and Treseder 2008). Much of Interior Alaska is underlain by permafrost and is water-logged, creating areas of high soil moisture and low nutrient availability due to anoxia reducing

microbial activity (Van Cleve et al. 1993; Rennenberg et al. 2009). Soil temperature and active layer depth are both likely proxies for net mineralization, since cold soils inhibit microbial activity (Van Cleve et al. 1993). The presence of shallow permafrost cools the soil and inhibits drainage so water collects both from weather events through the growing season as well as from the thawing ground. (Wrona et al. 2016). We obtained elevation, active layer depth, and time since fire from the Bonanza Creek LTER data catalog (Ruess et al. 2015; LTER data catalog 2017). We measured soil moisture (% vol; HH2, Delta-T Devices) and soil temperature (HANNA HI145) two times at five points across each site (four corners and the center for a total of ten measures each visit) after 5 days without rain, once in July and another in August of 2018. Due to weather events and lack of access to sites from poor road conditions after rains or damaged all-terrain vehicles, we did not have reliable soil measures from 2017. Since we were interested in relative soil moisture and temperature between sites, we used the 20 measurements per site from 2018 for all analyses. To measure canopy cover over each study ramet, we averaged three readings of a concave spherical densiometer measured 2 cm above the ramet, each reading taken 120° apart while kneeling. The above variables make up what we will refer to as "environmental variables" (elevation, active layer depth, stand age, soil moisture, and soil temperature).

Flowers on the study plants were counted as soon as they were distinguishable, in late May to early June. Blueberry shrubs can produce over 100 flowers and do not flower all at once, so to avoid double counting on return visits we marked each flower with paint. Flowers of other species in the vicinity may help or hinder berry production by attracting pollinators to an area where the insects otherwise may not go, or by competing with the *Vaccinium* ramet for those same insects. Other flowering species, common in the Interior Alaskan boreal forest, that overlap

in flowering times, include *Rhododendron groenlandicum, Chamaedaphne calyculata, Cornus canadensis,* and *Rubus chamaemorus*. We counted total floral resources, defined as all flowers of any species within a 1 m radius of the focal blueberry ramet or 0.5 m radius of the focal lingonberry ramet, during peak flowering of the *Vaccinium* as a measure of the potential for neighborhood plants to attract pollinators to the area or compete with focal plant flowers for resources. *R. groenlandicum* and *C. calyculata* produce many flowers per inflorescence and made up the bulk of non-*Vaccinium* floral neighbors. The timing of lingonberry overlapped with the flowering time of *R. groenlandicum* and *C. calyculata* more than blueberry.

We estimated pollen availability by collecting two pistils from conspecific flowers near each study ramet and estimating pollen loads on the stigmas under a microscope. We attempted to collect pistils during the peak flowering period of each species. Blueberry pistils were collected between June 4 and 26, 2017 and lingonberry pistils between June 11 and 26, 2017. Pistils were mounted on microscope slides in basic fuschin gel (Kearns and Inouye 1993) within a few days of collection. Following Spellman et al. 2015, a ramet was considered "well-pollinated" when the mean number of pollen tetrads on neighboring stigmas was greater than ten. Blueberries produce about 45 ovules per flower and lingonberries about 32 in Interior Alaska (Mulder and Spellman, unpublished data) so ten pollen tetrads could produce enough sperm to fertilize 100%, or nearly 100%, of ovules. It is unknown how many ovules must be fertilized for the plant to create a fruit. We quantified fruit set as the ratio of berries to flowers on a ramet.

2.3.4 Allocation measurements

Ramets, still with their leaves, were dried in an oven for 48 hours before leaves were removed for surface area and mass measurements. Berries from each reproductive plant were placed in a coin envelope while in the field and left in a drying oven for two weeks to ensure

complete desiccation. The biomass measurements were later used to asses proportion of resources allocated to leaves, stems, and berries between environment types.

For each ramet we investigated reproductive and vegetative allocation through the ratios of leaf mass : stem mass, flower number : leaf mass, and berry mass : leaf mass.

2.3.5 Statistical Analyses

We expected variables to be highly correlated, so to categorize the physical environment of the sites we used a principal component analysis (PCA) to sort the sites based on the average of the environmental variables: time since fire, elevation, soil moisture, soil temperature, and active layer depth. We used the mean calculated from other sites in place of missing values. We standardized the site averages to a mean of zero and standard deviation of one. The PCA was performed with the built-in R function princomp() (R Development Core Team). Values for both PCA axes were used as explanatory variables in the structural equation models.

We created a hypothetical structural equation model (SEM; Grace 2006) to assess direct and indirect effects of multiple variables on blueberry and lingonberry fruit production in 2017 (Figure 2.2). In our *a priori* model, we grouped several environmental variables into two model components: those primarily driven by geography (e.g., elevation) and those driven by stand history (e.g., time since fire). These correspond approximately to PCA1 and PCA2, respectively. We expected the number of berries produced to be strongly influenced by the number of flowers produced at the beginning of the season. The number of flowers and the number of berries, each ramet produced was expected to be related to canopy cover through the canopy's direct effect on light availability or through trees and tall shrubs indicating local growing conditions. Finally, we expected geography and stand history to influence the entire plant community in the area.

Prior to fitting the path model, we took the natural log of total floral resources, pollen load, number of flowers, and number of berries produced, to improve adherence to model assumptions. For both species, we ran a model that included data from all sites, but the explanatory power for the focal response variable, number of berries produced as measured by the R^2 values, was low (blueberry R^2 =0.31; lingonberry R^2 =0.09). To test for differences in plant responses by site type, we split our sites into two groups: one group with PC1 scores >0 (generally higher elevation sites with low soil moisture and high active layer depth [hereafter: upland]), and the other with PC1 scores <0 (generally low elevation with high soil moisture and low active layer depth [hereafter: lowland]). In all, we ran an SEM for each species with all ramets (2 models) and another for each species by splitting sites into upland (PC1 >0) and lowland groups (PC1 <0)(4 models), ultimately creating 6 models to compare. We did not force the regression equations in the SEM through zero in order to avoid interpreting beyond what we sampled. The SEM was performed through the Analysis of Moment Structure (AMOS version 25.0, Arbuckle 2012) statistical package using maximum likelihood estimation. We assessed model fit based on the ratio of minimum discrepancy to degrees of freedom (CMIN/df; ratio is between 1 and 5), root mean square error of approximation (RMSEA; lower 90% confidence interval is close to zero, 0.05 or lower), and the comparative fit index (CFI >0.90) (Grace et al. 2012).

We calculated the coefficient of variation in flower production and berry production for each species at all 17 sites and used a Student's t-test to test for significant differences in the two species overall levels of reproduction. To check for differences in berry production across sites we performed a one-way ANOVA of fruit set rates by site. We used R-squared values to examine the relationships of biomass ratios with canopy or stand history; this was done for each

species singly and for each species in upland and lowland. We checked for differences in fruit set by site through one-way, fixed variable ANOVAs with the anova() function. All statistical analyses other than SEM were performed using base packages in R version 3.3.2 (R Development Core Team).

2.4 Results

2.4.1 Berry production

The variation in production of flowers and berries differed considerably across all 17 sites with blueberry ramets generally more variable than lingonberry ramets. However, while variation in flower production was greater in blueberries than in lingonberries (difference in coefficient of variation: $t = -5.79$, $p = <0.001$), there was less evidence for a difference in variability in berry production ($t = -1.82$, $p = 0.096$; Appendix B). Across all sites, 72% of blueberry flowers and 39.5% of lingonberry flowers were defined as well pollinated (Figure 2.3a; mean pollen load was 26 and 12 tetrads, respectively). Blueberry flowers produced fruit 24% of the time and for lingonberry 31% (Figure 2.3b). Site explained significant variation in fruit set in both blueberry (ANOVA: $F_{(16,165)}=3.74$, $p <0.001$) and lingonberry ($F_{(16,168)}=5.66$, $p <0.001$). The mean number of berries produced per ramet at each site ranged from 0.08 to 9.83 (total berries per site: 0-118) and 0 - 1.92 (total: 0-23) for blueberries and lingonberries, respectively (Figure 2.3c).

2.4.2 PCA and model fit

The PCA split the majority of the sites into two distinct groups along principal component 1 (Figure 2.4). PC1 was positively correlated with elevation and active layer depth and negatively correlated with soil moisture. The sites with negative PC1 scores we termed lowland and those with positive PC1 scores were termed upland. Sites GSM4 and BFY6 were

near the center but both fell below PC1=0 so we grouped them with the lowland sites. PC2 was positively associated with stand age and soil temperature (Table 2.1). Principal component 1 (PC1) explained 45% of the variation and PC2 explained 34% in the PCA (Figure 2.4). We used both the PC1 and PC2 scores in the model, calling them site geography and stand history respectively.

Our multi-group SEM with all the ramets of each species included had a CMIN/df of 4.290 (fit: 1-5), CFI was 0.806 (fit: >0.90), and RMSEA was 0.093 (90%CI: 0.070 –0.118; fit: 0.05 inclusive) (Figure 2.5). The models explained 31% of the variation in blueberry fruit production but only 9% of lingonberry fruit production. With the ramets divided by upland and lowland designation, fit statistics improved: CMIN/df was 2.735, CFI was 0.902 and RMSEA was 0.068 (90% CI: 0.050 - 0.086); more paths were significant, and R^2 values improved (Figure 2.6).

2.4.3 Resource and pollen limitation

When looking across all sites, pollen loads were less important to blueberry production than lingonberry fruit production (Figure 2.5). However, when the ramets were divided into upland and lowland the positive relationship between berry production and pollen was only seen in the lowland sites while in upland sites berry production was negatively affected by canopy cover (Figure 2.6).

2.4.4 Direct and indirect effects of environment on berry production

The single greatest positive influence on berry production in all six models was flower production. In the SEM that included all sites (Figure 2.5) the only significant effect of canopy cover was on blueberry flower production. Median canopy cover over blueberries at lowland sites was 29% while for lingonberries it was 33%. Upland sites in our study tended to have more

canopy closure reflecting a greater percentage of broadleaf trees. Canopy cover had differing effects on flower production depending on the species and environment. The effect of canopy cover on flower production was only significant in the upland sites but the effect was negative in blueberries and positive in lingonberries. Canopy cover negatively influenced berry production at upland sites and positively influenced berry production in lowland sites for both blueberry and lingonberry whereas pollen significantly influenced berry production only at lowland sites (Figure 2.6). Stand history (PC2) was only significant to flower production for the lowland lingonberry ramets. Geography (PC1) had a significant positive effect on flower production in lowland blueberry and upland lingonberry.

Pollen load was significant to fruit production in lowland but not in upland sites (Figure 2.6). The lowland lingonberry model was the only one where both components of the pathway from total floral resources to pollen and pollen to berries was significant. Based on the pollen averages, upland lingonberry ramets well pollinated (>10 tetrads) 55% of the time, lowland lingonberry ramets 24%, upland blueberry ramets 83%, and lowland blueberry ramets 61%. Canopy cover had a negative influence on berry production in upland sites but a positive influence in lowland sites. Stand history had a positive significant effect on berry production in lowland but was not significant in upland.

The top three variables, in terms of the sum of all effects, on the number of berries produced were flower production, stand history, canopy cover or pollen load for all the models in Figure 2.6 (Table 2.2). When adding the absolute values (to determine which variables played the largest role), the top three variables in all models still included flower production, stand history, and canopy cover but included site geography instead of pollen load (Table 2.2). When looking at all sites, after flower production, pollen load was the greatest influence on berry

production. However, when ramets were split by site geography we found canopy cover and stand history were consistently the greatest influence on Interior Alaskan blueberry production while pollen was more significant to lingonberry production in 2017 (Figure 2.6, Table 2.3).

2.4.5 Correlation between environmental variables

We predicted stand history would be the greatest influence on resource availability due to the influence on canopy cover. Stand history (PC2) had no effect on canopy cover in the lowland sites but was a strong positive predictor of canopy cover in the upland sites (Figure 2.6a-d). In upland sites, the only significant effect stand history had on berry production was through canopy cover. Thus, ultimately a negative effect. Site geography (PC1) had a significant positive effect on canopy cover in all four species/environment SEMs but was never significant to total floral resources. Total floral resources only had a significant effect on pollen load in lowland lingonberry ramets (Figure 2.6d). Even with the observations divided by the "Geography" principal component (PC1: elevation, moisture, active layer depth), thereby limiting the range within each model, geography still had significant effects on other model components.

2.4.6 Allocation given canopy cover

When ramets from all sites were included, the strongest relationship, as measured by R^2, between biomass ratios and canopy cover was that between leaves and plant size (leaf mass : stem mass) for lingonberries ($R^2 = 0.11$, Table 2.4). When we divided the ramets into the upland and lowland groups the relationships between biomass allocation and canopy cover, when significant, had R^2 values more than double those that were significant when all sites were included. The upland ramets (Table 2.5a) had more significant relationships with larger R^2 values between biomass ratios and canopy cover than the lowland ramets (Table 2.5b). As canopy cover increased, the relative amount of investment in reproductive biomass, whether flower number or

berry mass, decreased compared to vegetative biomass. In both blueberries and lingonberries in upland sites investment in leaves given the mass of the stem (leaf mass : stem mass) decreased as canopy cover increased. Canopy cover explained more than twice as much of the change in allocation in lingonberry as it did in blueberry (lingonberry R^2 =0.24 blueberry R^2 =0.10). While allocation within individual ramets may change with canopy cover, lingonberry populations as a whole do not change flowering rates with canopy cover ($p > 0.99$) while blueberry population in Interior Alaska does respond to changes in canopy ($p = 0.007$, Figure 2.7).

2.5 Discussion

Our primary goal in this research was to assess pollen versus resource limitation on berry production of blueberry and lingonberry in the boreal forest of Interior Alaska. We found that pollen and resource limitation differed between species and location. Lower elevation, wetter sites with shallower active layers tended to be more pollen limited than the upland, drier sites. Blueberry plants were less pollen limited than lingonberry plants. The differences between species, and among environmental conditions, suggest that blueberries and lingonberries have divergent life history traits that may drive their response to changes in environmental conditions, such as increases in fire frequency and extent. Our work suggests that blueberry and lingonberry reproduction and allocation patterns were affected by different limitations according to habitat type. Canopy cover was a strong predictor of berry production and allocation in upland sites, most likely as a proxy for light availability or other resource competition from the dominant trees. Lowland sites were more pollen limited but we did not find a strong predictor of reproductive or vegetative investment in either species at these sites. If the differences in blueberry and lingonberry reproduction and allocation we found in the two habitats is a long-

term pattern, the expected changes in boreal forest fire regime and subsequent effects on soils may change *Vaccinium* reproductive limitations in different ways across the boreal forest.

2.5.1 Resource versus pollen limitation

Light availability, as indicated by canopy cover, was a strong influence on both blueberry and lingonberry fruit production. The negative correlation between canopy cover and berry production in upland sites was likely light limitation, though competition from tree species for nutrients and water was also likely influencing the relationship. Light limitation would explain the increased biomass investment in stems compared to leaves in upland sites as canopy cover increases. *Vaccinium* ramets may be attempting to grow taller or wider to outcompete neighbors for the limited light. The positive correlation between canopy and berries in lowland sites was more difficult to interpret but could be indicative of good growing conditions at the small scale around individual ramets. The drastically different pattern between stand history and canopy cover between upland and lowland may support this. Stand history had a significant, positive effect on canopy cover in upland sites — the longer it had been since a fire, the more shrubs and trees had grown around the *Vaccinium*. However, stand history had no significant effect on canopy cover in lowland sites. This difference in regeneration pattern was also found in the boreal black spruce forests of Quebec (Harper et al. 2002). In that study, less productive sites, those with excess moisture, had slower rates of regeneration and a different community structure develop than sites with drier conditions. In our study, there was little change of tall growth in the lowland sites with time since fire. Therefore, when we did measure tall growth in the lowlands it was then indicative of good growing conditions, not time.

Lingonberries were additionally affected by pollen load (Tables 2 and 3). Pollen may limit lingonberry production more than blueberry production due to lingonberry flowers' low

levels of self-pollination. In a pollinator study in Interior Alaska, when pollinators were denied access to flowers blueberry still set fruit 24% of the time while lingonberries only set fruit 6% compared to flowers with pollinator access (Spellman et al. 2015; CPH Mulder, unpublished data). Regardless of this difference between the species, the direct pathway between pollen load and fruit production was only significant in lowland sites. This suggests that while lingonberries were more pollen limited than blueberries, ramets at lower elevations (with greater soil moisture and shallower active layer depth), whether blueberry or lingonberry, have a greater potential for pollen limitation than ramets in upland sites.

Canopy cover at lowland sites did not explain a significant proportion of variation of flower production. The lack of correlation between flower production and canopy cover in lowland sites may be due to opposing canopy influences at the lowland sites. Decreases in flower production of the globe huckleberry (*V. globulare*) in Montana were attributed to resource limitation above 30% canopy closure (Martin 1983). We also noted that blueberry fruit set (the ratio of berries : flowers) increases with canopy cover at lower elevations which lends support to canopy cover as a general indicator of site quality in lowlands.

2.5.2 Total floral resources and pollen limitation

As a whole, blueberries were better pollinated than lingonberries, though both species showed evidence of pollen limitation in the lowland models. Previous work by Spellman et al. (2015) found canopy cover, total floral resources, and air temperature were all significant in explaining *V. vitis-idaea* pollination rates in black spruce sites but not mixed deciduous sites (analog to our lowland and upland delineations). Due to the similarities in outcomes between my study and other studies of pollinators and pollination in the Interior we think our findings in this aspect are robust.

2.5.3 Study limitations

All measurements, except soil moisture and temperature, took place within the 2017 growing season. The 2017 growing season in Interior Alaska was warmer than normal. Particularly in June, the Fairbanks International Airport had multiple record-high temperature and precipitation days (USDA: Alaska Agricultural Statistics 2018 Annual Bulletin). However, first flowering dates in 2017 were June 4 for blueberry and June 11 for lingonberry. These fall in the middle of first flowering dates documented in 2013, 2014, and 2015 of May 24 to June 11 and June 4 to 21 for blueberry and lingonberry respectively (CPH Mulder unpublished data).

Additionally, the different life history strategies of blueberries and lingonberries may limit our conclusions. Both blueberries and lingonberries are clonal but *V. vitis-idaea* can form dense mats of genetically identical ramets that share resources (Hultén 1965). The trade-offs between vegetative and reproductive growth may not be occurring within a single ramet but across many connected ramets in an area. We did not measure the extent of the spread of the clones or their ability to trade off reproductive and vegetative growth communally. Additionally, lingonberry is evergreen, so resource competition between vegetative and reproductive growth within a ramet takes place between berries and only the leaves produced within that growing season (Poorter and Nagel 2000). We included all leaves from the lingonberry ramets in our biomass ratios.

Patterns in berry production and resource allocation were stronger in the upland sites. Lowland sites encompassed a greater range of site conditions so it appears that environmental limitations were driven by something we missed in our study. Studies of *Vaccinium* species and boreal plant communities in Sweden have found soil pH and soil microbial activity play a role in community composition and *Vaccinium* biomass allocation (Tyler 1989; Kumordzi et al. 2016).

Additionally, Interior Alaska contains a variety of wetland types each made of a variety of combinations of water movement, soil type, and permafrost, all of which affect the plant communities above them (Hall et al. 1994; McConnell et al. 2013). Future work in Interior Alaska to elucidate the controls on *Vaccinium* production should follow examples of studies in Fennoscandia by including soil pH, direct measures of nutrient cycling, and wetland conditions.

2.5.4 Potential changes in berry production

The significance of canopy cover on berry production in the uplands leads to two potentially contrasting outcomes for future berry production in Interior Alaska. The change in forest fire dynamics caused by climate change is causing fires to increase in size, severity, and frequency (Weber and Flannigan 1997; Kasischke and Turetsky 2006; Kasischke et al. 2010). The increase in size and frequency will lead to a lower median stand age, generating canopy cover in the range most conducive to berry production (<30%). Other research in Russia and Montana has found berry production peaks 10–20 or 25–60 years after a wildfire, respectively (Marten 1980; Mironov 1984 in Nelson et al. 2008). Lowland sites may still be limited by pollinators or other resources not associated with canopy but upland could see an increase in berry production with more fire releasing the resource limitations caused by competition from canopy. At least for the short term, more frequent, large fires could increase the extent of boreal forest with a canopy structure favorable for berry production. However, fires are also changing in severity. More severe fires consume not just the plant communities above the soil but much of the soil organic layer itself (Kasischke and Turetsky 2006), changing the immediate and long-term successional dynamics of the forest (Rupp et al. 2002). More severe and more frequent fires create a new stable state of succession that instead of transitioning from hardwoods to spruce stays hardwood until the next fire (Flannigan et al. 2005; Mack et al. 2008; Johnstone et al. 2010).

Increased homogeneity of boreal forest environments due to changes in fire may lead to greater boom and bust cycles in local berry production. Already, while the average number of berries produced each year has stayed approximately the same over the last few decades, variability in timing of blueberry production has increased (CPH Mulder, unpublished data, 2018). Due to the importance of berries to both human and animal diets around Interior Alaskan boreal forest, those who work to predict long term changes in plant and animal distributions in Alaska should include reproductive changes, not just vegetative changes, as the boreal habitat responds to climate change.

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2.7 Figures

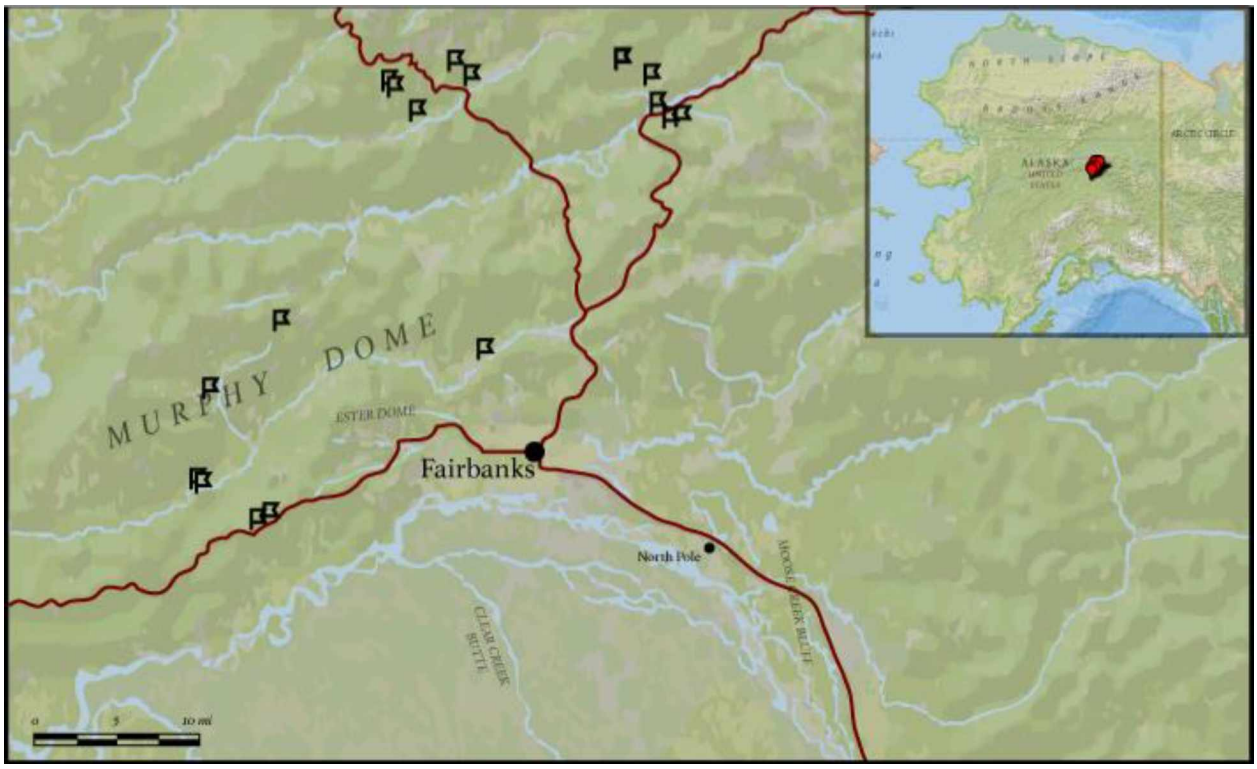

Figure 2.1 The 17 sites within the Bonanza Creek LTER regional site network used in this study. All sites are within 70 km of Fairbanks (64.843611, -147.723056) and represent a variety of black spruce forest types. Map credit: GPSvisualizer.com, Megan Perra.

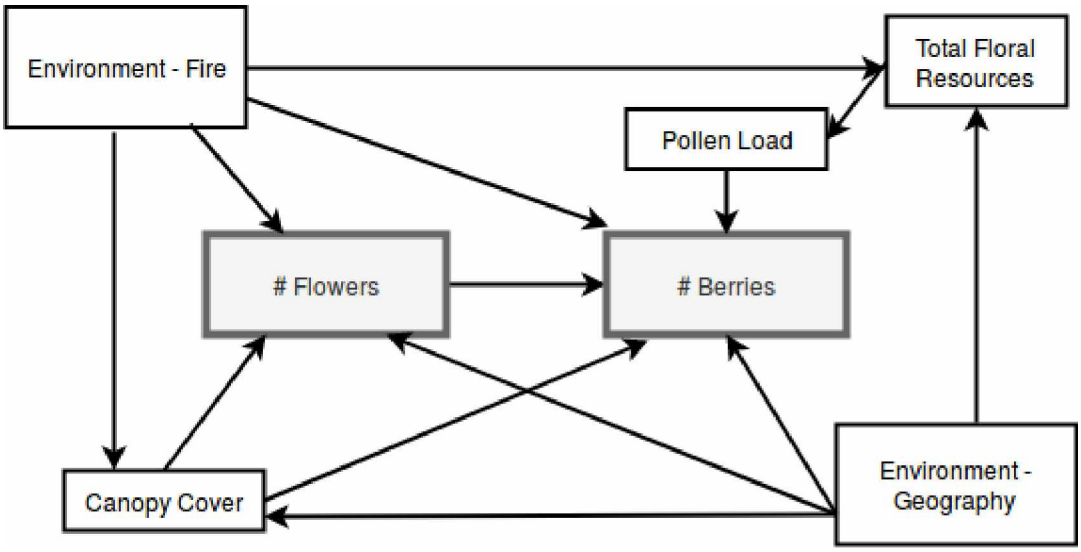

Figure 2.2 Hypothesized structural equation model. Response variables are grey. "Environment - Geography" consists of correlated factors that differ primarily by position in the landscape, "Environment - Fire" encompasses fire history. Other predictive variables were measured at each *Vaccinium* ramet.

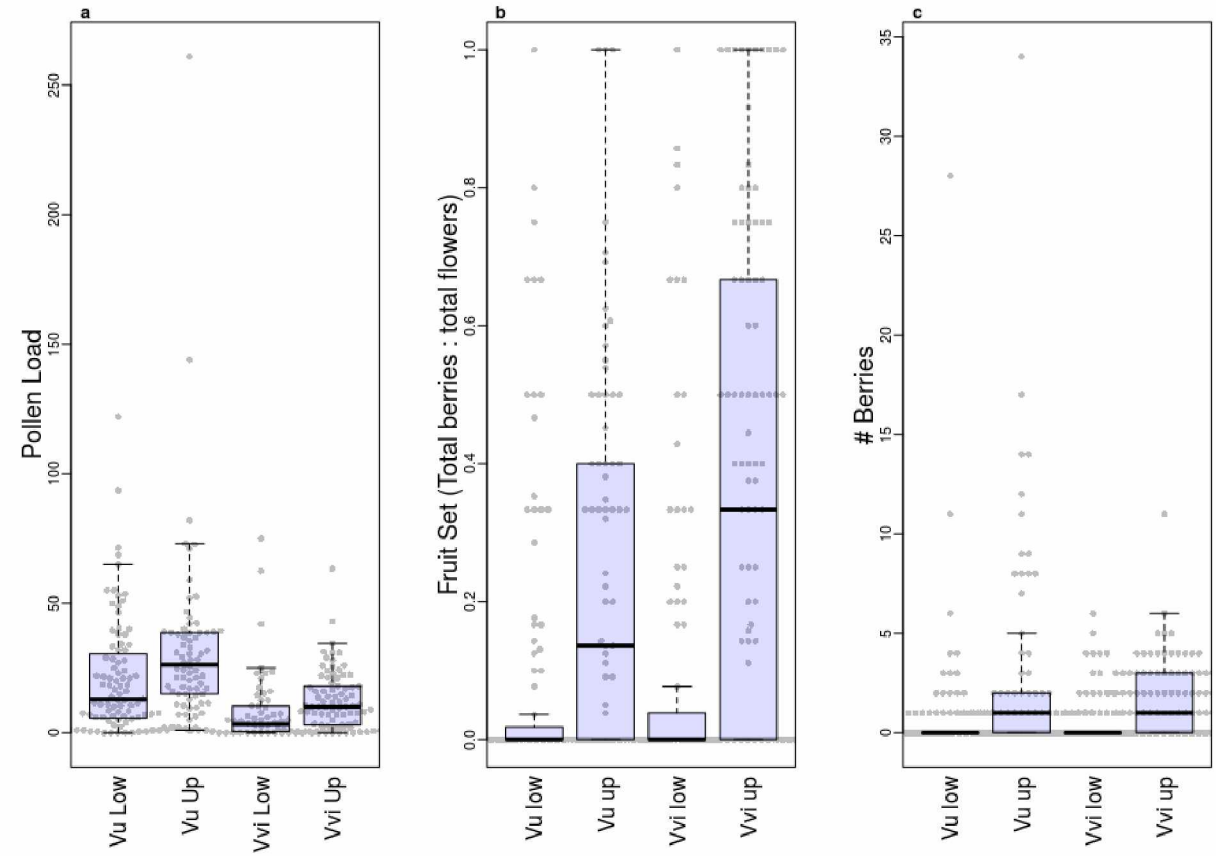

Figure 2.3 a) Pollen load, b) fruit set, and c) number of berries produced, per ramet from all blueberry (*Vaccinium uliginosum*) and lingonberry (*V. vitis-idaea*) ramets. X-axis is *V. uliginosum* lowland, *V. uliginosum* upland, *V. vitis idaea* lowland and *V. vitis-idaea* upland. Boxplot midline is the median, the box is the third and first quartile, the whiskers extend up to 1.5 times the interquartile range from the top of the box to the furthest datum within that distance. Grey dots are the raw data.

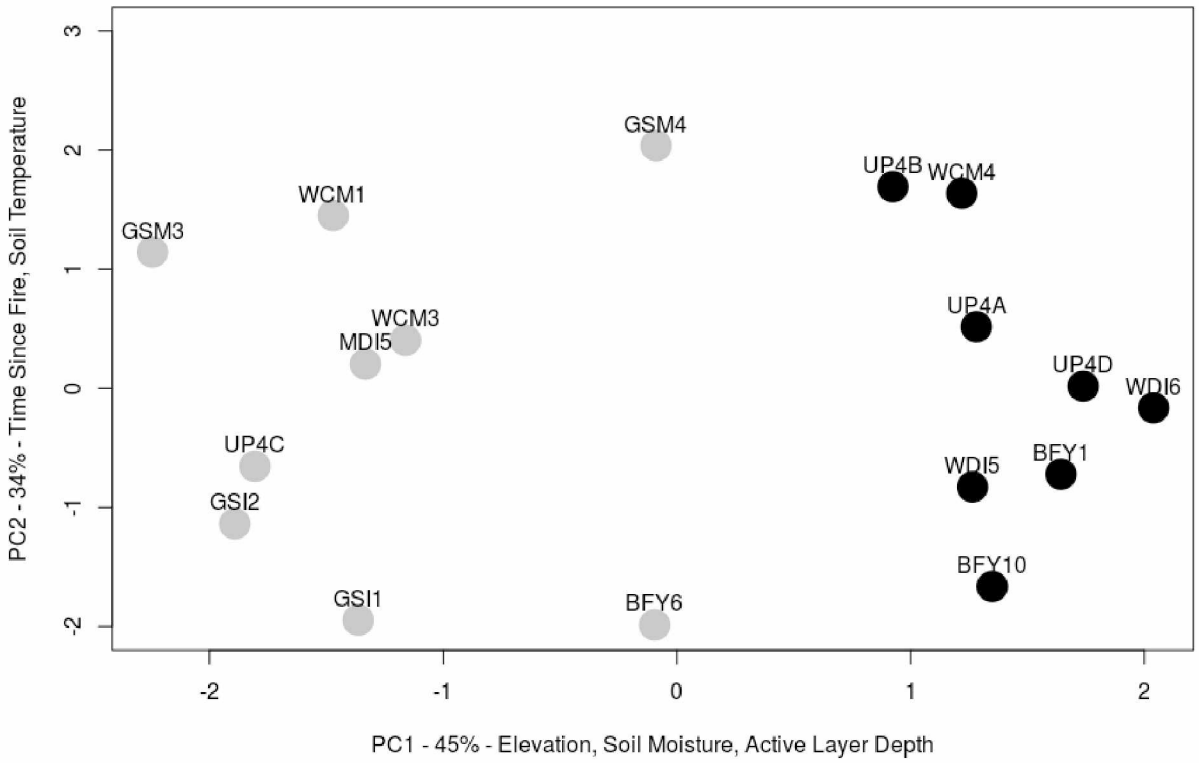

Figure 2.4 PCA of environmental variables measured to encompass a 50 x 60m site. On PC1 elevation and active layer depth were positively correlated while soil moisture was negatively correlated. Sites were divided above and below PC1 =0 (grey and black dots) for analysis in the structural equation models. Further details about the sites in Appendix A.

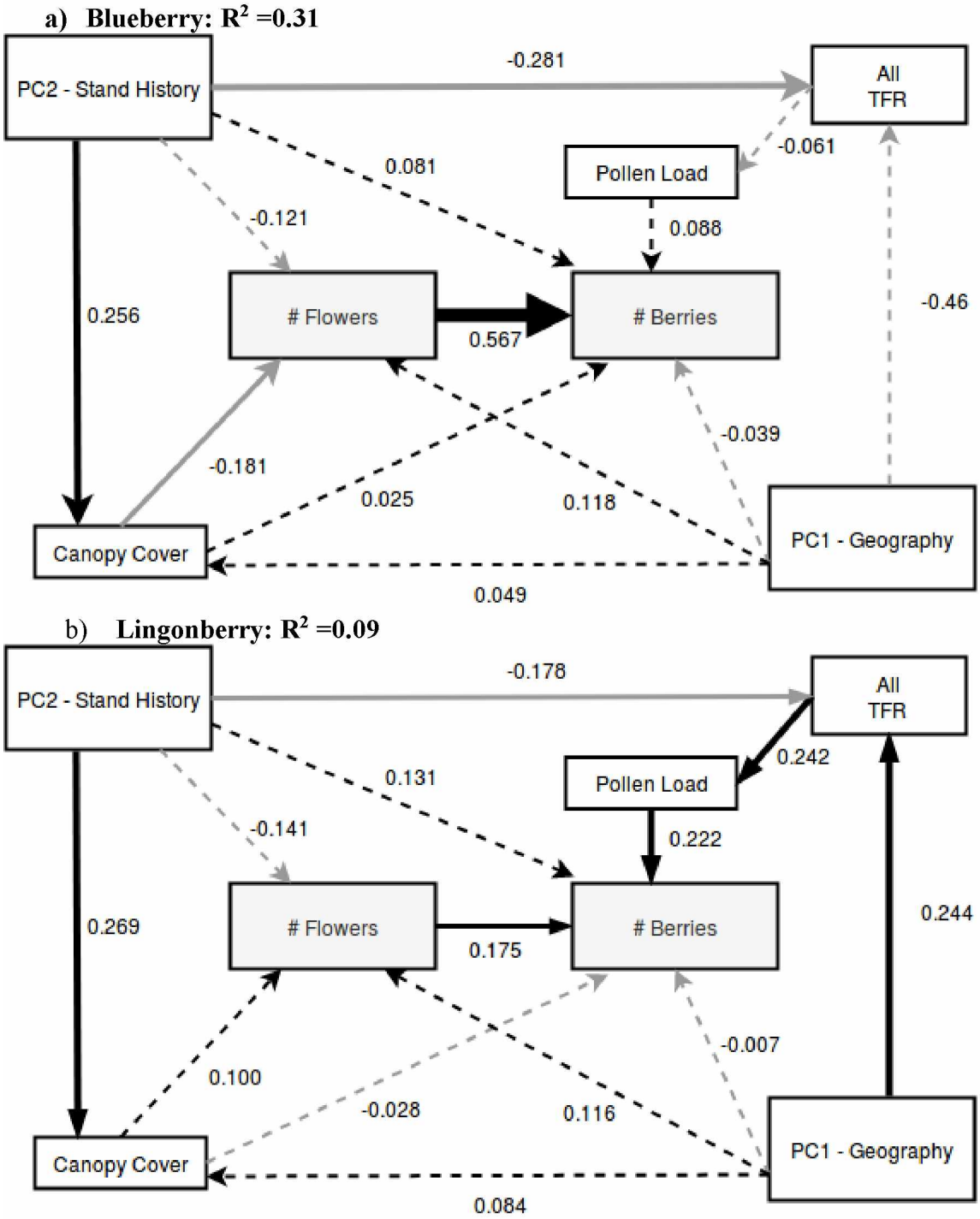

Figure 2.5 Structural equation model pathways. a) all blueberry (*Vaccinium uliginosum*) ramets, n =186; b) all lingonberry (*V. vitis-idaea*) ramets, n =195. Grey boxes are the response variables. Solid lines represent significant pathways ($p<0.05$), while dashed lines are non-significant. Black lines represent positive pathways, while grey lines are negative pathways. Path coefficients are the standardized estimates from the multi-group structural equation model. R^2 is for the number of berries

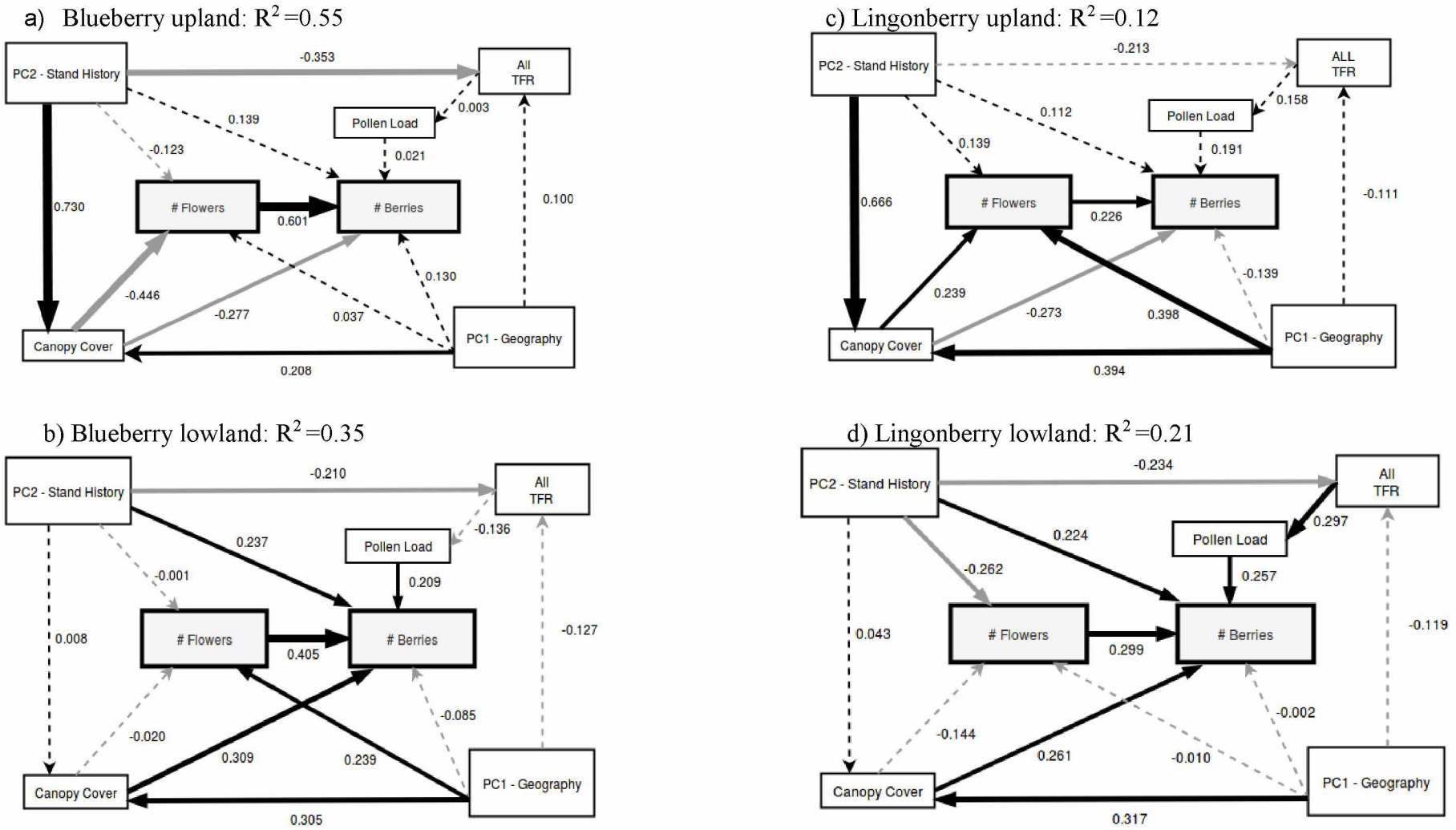

Figure 2.6 Final structural equation model pathways. a) upland blueberry, n =80; b) lowland blueberry, n =106; c) upland lingonberry, n =97; d) lowland lingonberry, n =98. Grey boxes are the response variables. Solid lines represent significant pathways, while dashed lines are non-significant. Black lines represent positive pathways, while grey lines are negative pathways. Path coefficients are the standardized estimates from the SEM. $R^2$is for the number of berries.

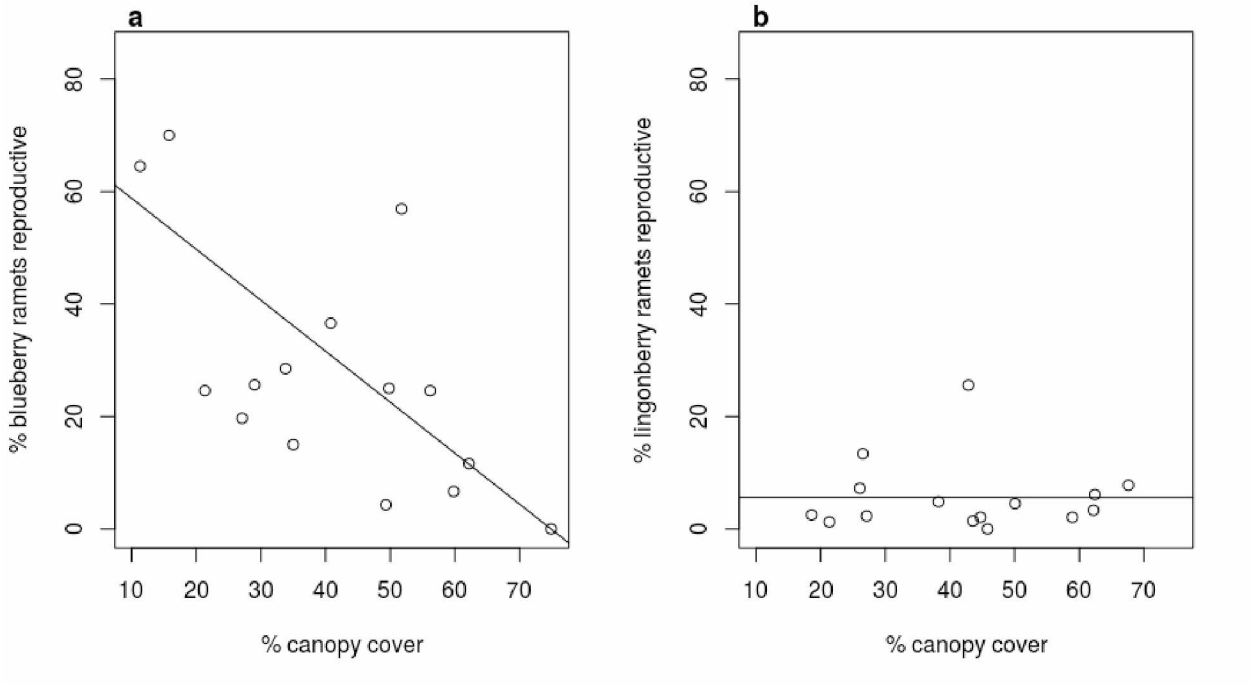

Figure 2.7 The percentage of reproductive ramets at each site by the percentage of canopy cover at the site. a) blueberry (*V. uliginosum*) p =0.007, R^2 = 0.37, n =15; b) lingonberry (*V. vitis-idaea*) p =0.998, n =15.

2.8 Tables

Table 2.1 PCA loadings. Principal components 1 and 2 were included in the structural equation model and referred to as Site Geography and Stand History, respectively.

	PC1	PC2
Soil temperature	---	**0.651**
Soil moisture	**-0.534**	-0.157
Active layer depth	**0.563**	-0.266
Age	-0.186	**0.659**
Elevation	**0.595**	0.216

Table 2.2 The top three combined (indirect + direct) effects, both additive and absolute value, on number of berries in each SEM shown in Figure 2.5.

Blueberry	Direct	Additive	Abs. value	**Lingonberry**	Direct	Additive	Abs.value
Flowers	0.567	0.567	0.567	Pollen	0.222	0.222	0.222
Pollen	0.088	0.084	--	Flowers	0.175	0.175	0.175
Canopy	0.025	-0.077	0.128	Stand History (PC2)	0.131	0.094	0.177
Stand History (PC2)	0.081	--	0.184	--	--	--	--

Table 2.3 The top three combined (indirect + direct) effects, both additive and absolute value, on number of berries in each SEM shown in Figure 2.6.

	Blueberry	Direct	Additive total	Abs. value sum	**Lingonberry**	Direct	Additive total	Abs. value sum
Upland								
	Flowers	0.601	0.601	0.601	Stand History (PC2)	-0.213	-0.334	0.469
	Canopy	-0.277	-0.545	0.545	Flowers	0.226	0.226	--
	Stand History (PC2)	0.139	0.219	1.015	Pollen	0.191	0.191	--
	--	--	--	--	Stand History (PC2	0.213	--	0.469
	--	--	--	--	Site Geography (PC1)	0.139	--	0.361
Lowland								
	Flowers	0.405	0.405	0.405	Flowers	0.299	0.299	0.299
	Canopy	0.309	0.301	0.317	Pollen	0.257	0.257	--
	Stand History (PC2)	0.237	0.245	--	Canopy	0.261	0.218	0.304
	Site Geography (PC1)	0.085	--	0.283	Stand History (PC2)	0.224		0.333

Table 2.4 The relationships between biomass ratios and canopy cover for all blueberry (*Vaccinium uliginosum*) and (*V. vitis-idaea*) ramets. Parameter estimate and p-values for all relationships. Significant ($p < 0.05$) relationships are in **bold** and contain the adjusted R^2 value.

Response variable ratios	Blueberry	Lingonberry
Leaf mass : stem mass	-0.0002, p =0.71	**-0.0213, p <0.001, R^2 =0.11**
# flowers : leaf mass	-0.0893, p =0.084	**-0.4362, p =0.003, R^2 =0.04**
Berry mass : leaf mass	-0.0005, p =0.20	0.0004, p =0.49

Table 2.5
The relationships between biomass ratios and canopy cover for blueberry (*Vaccinium uliginosum*) and lingonberry (*V. vitis-idaea*) ramets in upland and lowland sites. Parameter estimate and p-values for all relationships. Significant ($p<0.05$) relationships are **bold** and contain the adjusted R^2 value.

a) Upland

Response variable ratios	Blueberry	Lingonberry
Leaf mass : stem mass	**-0.0015, p =0.003, R^2 =0.10**	**-0.0079, p <0.001, R^2 =0.24**
# flowers : leaf mass	-0.0584, p =0.342	0.0367, p =0.73
Berry mass : leaf mass	**-0.0021, p <0.001, R^2 =0.16**	-0.0014, p =0.205

b) Lowland

Response variable ratios	Blueberry	Lingonberry
Leaf mass : stem mass	0.0009, p =0.364	-0.006, p =0.444
# flowers : leaf mass	-0.0649, p =0.476	**-0.6259, p =0.0391, R^2 =0.04**
Berry mass : leaf mass	0.0006, p =0.348	0.0007, p =0.280

2.9 Appendices

Appendix A

Site names and descriptions. Upland sites are highlighted grey, lowland sites are white.

Site	Lat	Long	Elevation	Age	Soil Moisture	Primary Canopy
BFY1	65.119	-147.429	497	13	Subxeric	Open
BFY10	65.118	-147.449	425	13	Subxeric/Mesic	Open
BFY6	65.13	-147.477	210	13	Mesic	Sapling Hardwood
GSI1	64.8	-148.413	144	51	Mesic	Black Spruce
GSI2	64.802	-148.42	129	51	Subhygric	Open Black Spruce
GSM3	64.916	-147.832	188	175	Subhygric	Black Spruce
GSM4	64.942	-148.253	504	85	Subxeric/Mesic	Black Spruce
MDI5	64.882	-148.398	215	59	Mesic	Open Black Spruce
UP4A	64.768	-148.298	490	100	Subxeric	Black Spruce
UP4B	64.771	-148.273	400	200	Subxeric	Black Spruce
UP4C	65.153	-147.491	233	130	Subxeric	Black Spruce
UP4D	65.169	-147.55	620	100	Subxeric	Black Spruce
WCM1	65.124	-147.973	246	190	Subxeric	Open Black Spruce
WCM3	65.154	-147.863	271	190	Subxeric	Black Spruce
WCM4	65.167	-147.894	459	190	Subxeric	Black Spruce
WDI5	65.145	-148.018	477	46	Subxeric	Hardwood
WDI6	65.148	-148.026	505	46	Subxeric	Hardwood

Appendix B

Coefficient of variation in flowers produced and berries produced for blueberries (*Vaccinium uliginosum*) and lingonberries (*V. vitis-idaea*) in each site and overall.

	CV Number of Flowers		CV Number of berries	
	Blueberry	Lingonberry	Blueberry	Lingonberry
BFY1	0.208	0.444	0.949	0.782
BFY10	0.553	0.550	1.160	0.695
BFY6	0.999	0.540	2.486	1.595
GSI1	0.631	--	1.310	--
GSI2	0.923	0.853	2.663	3.464
GSM3	1.407	0.431	2.462	1.236
GSM4	1.359	0.973	1.954	2.335
MDI5	0.724	0.532	3.464	1.031
UP4A	0.883	0.379	1.370	1.095
UP4B	1.115	0.247	0.729	0.692
UP4C	0.726	0.480	1.605	--
UP4D	0.850	0.479	1.168	0.841
WCM1	1.415	0.675	3.464	--
WCM3	1.410	0.410	2.533	--
WCM4	0.584	0.336	1.477	1.172
WDI5	0.849	0.487	1.841	1.642
WDI6	--	0.564	--	1.407
Overall	0.868	0.334	1.570	0.789

Chapter 3 Conclusion

My research illustrated the spatial variability of resource and pollen limitation on blueberry and lingonberry reproduction and biomass allocation in Interior Alaskan black spruce forests. I used principal components analysis, structural equation models, linear regressions and ANOVAs to demonstrate the presence of two distinct habitat types with differing limitations on *Vaccinium* berry production. This project is one step toward assessing future food security and access to Alaska Native traditional food resources.

Berry plants go through a process more than one year long to reproduce: from developing a bud to flowering to fruit ripening. The blueberries and lingonberries produced at the end of one summer may then spend another nine months as a food source for local animals over the winter (CPH Mulder, unpublished data). At many stages in the reproductive cycle a ramet may abort reproductive processes (Figure 3.1). The greatest single determinant in whether any particular ramet in Interior Alaska in 2017 successfully produced a fruit was whether it attempted to reproduce in the first place, something I only touched on. In Yukon, Canada the greatest single determinant of whether a ramet will produce fruit is the amount of rain in May the year before flowering (Krebs et al. 2009). As far as I'm aware, no such interannual studies have taken place in Alaska. In 2017, of all the ramets in all my sites only 12% of blueberry and 1.7% of lingonberry ramets successfully produced at least one fruit. This thesis focused on how habitat type affected two of the later stages: whether or not a flower got pollinated (more exactly, whether pollen transfer in the area was high enough to allow fruiting), and how many of those flowers became fruits. Since I was less able to explain variability in reproduction in lowland than in upland habitats, I will now briefly focus on lowland conditions.

Lowland sites had almost twice the level of variation along PC1 as the upland sites. Some of the strength in explaining berry production or resource allocation may have been lost by grouping such disparate sites together. The lowlands of Interior Alaska are wetter than the uplands but the moisture in the lowlands comes in a variety of forms. Fens, bogs, and swamps are all habitats with water-logged soils but the water, soil, and plant community develop differently in each one. Future work should consider the role of wetlands and soil chemistry in the reproductive limitation and allocation in *Vaccinium.*

While the average number of berries produced around Interior Alaska has not changed in the last few years the amount of variation in berry production has increased (Hupp et al. 2015). Berry pickers perceive that berry boom-bust cycles are growing more extreme. I was inspired to study this topic after eavesdropping on two women before a collaborator meeting early in my master's program. They were discussing the traditional ethic of picking only what you need but if berry production varies so much from year to year, should they pick enough for one winter or two? My work does not directly predict long-term patterns in berry production, like these women were discussing, but I hope as we continue to research berry plants in Alaska our increased grasp of blueberry and lingonberry responses to their local environment can help us build a better understanding of fruit production and thus local food security.

3.1 References

Hupp, J., Brubaker, M., Wilkinson, K. and Williamson, J. 2015. How are your berries? Perspectives of Alaska's environmental managers on trends in wild berry abundance. Int. J. Circumpolar Health. **74**(1): 28704.

Krebs, C. J., Boonstra, R., Cowcill, K., and Kenney, A.J. 2009. Climatic determinants of berry crops in the boreal forest of the southwestern Yukon. Botany. **87**(4): 401-408.

3.2 Figure

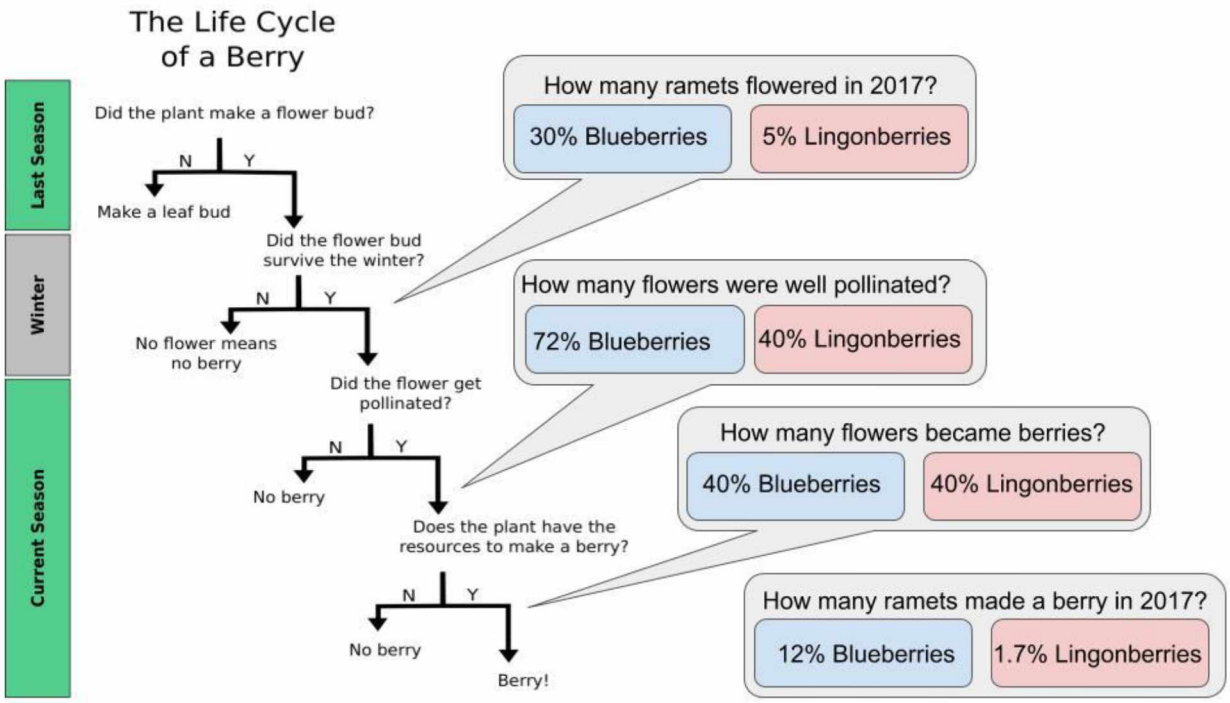

Figure 3.1 A flowchart of the steps in the berry production process and percentages of blueberry (*Vaccinium uliginosum*) and lingonberry (*V. vitis-idaea*) ramets that successfully completed that step in 2017.